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## Modulation by steroid hormones of a “sexy” acoustic signal in an Oscine species, the Common Canary *Serinus canaria*

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### ABSTRACT

The respective influence of testosterone and estradiol on the structure of the Common Canary *Serinus canaria* song was studied by experimentally controlling blood levels of steroid hormones in males and analyzing the consequent effects on acoustic parameters. A detailed acoustic analysis of the songs produced before and after hormonal manipulation revealed that testosterone and estradiol seem to control distinct song parameters independently. The presence of receptors for testosterone and estradiol in the brain neural pathway controlling song production strongly suggests that the observed effects are mediated by a steroid action at the neuronal level.

**Key words:** Oscines, Common Canary, song, steroid hormones.

### INTRODUCTION

In vertebrates, steroid hormones produced by the gonads and circulating in the blood play a key role in modulating behaviors associated with reproduction. In the Common Canary *Serinus canaria* (hereafter called canary), song expression varies across seasons and is correlated with important variations in testosterone levels in the blood (Nottebohm et al. 1987, Leitner et al. 2001, 2002). The songs, produced by males, are composed of different syllables sequentially repeated in phrases. As in all other Oscine species, the production of song by the canary is controlled at the cerebral level by a network of interconnected brain nuclei: the so-called caudal motor pathway within the song control system (Nottebohm et al. 1976). This neural pathway is steroid sensitive: all the nuclei express receptors for androgens, e.g. testosterone, (Arnold et

al. 1976, Brenowitz and Arnold 1992, Nastiuk and Clayton 1995, Gahr and Metzdorf 1997, Metzdorf et al. 1999) and the highest nucleus of the pathway – the HVC, which controls song organization (Yu and Margoliash 1996) – also contains receptors for estrogens, e.g. 17 $\beta$ -estradiol (Gahr et al. 1993, Metzdorf et al. 1999). Furthermore, the production of estrogens in the brain is also important, as the enzyme aromatase, which converts androgens into estrogens, is expressed and is active in many brain areas, including one adjacent to the nucleus HVC (Schlinger and Arnold 1992a, b, Balthazart et al. 1996, Shen et al. 1995, Metzdorf et al. 1999).

### MATERIALS AND METHODS

In order to assess how steroid hormones influence canary song structure and to determine whether testosterone has a direct effect on song parameters or an indirect effect *via* its estrogenic metabolite, we performed hormonal manipulations in sexually mature male canaries. We subcutaneously implanted

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either testosterone plus Fadrozole, an inhibitor of estradiol synthesis (group T + FAD) or testosterone plus a placebo (group T + Placebo) in 11 males, and compared the songs produced before and after implantation. After implantation, the song behavior was followed for three weeks.

### RESULTS

For hormone measurements, blood samples were taken from the wing vein of all birds before and at several times after implantation. As expected, the levels of testosterone increased after implantation in animals of both groups and this increase was higher in the birds where conversion of testosterone into estradiol was inhibited, thus showing the efficiency of the experimental procedure.

A detailed acoustic analysis performed on song structure revealed that some parameters that we studied were not sensitive to steroid hormones, but others appeared to be testosterone-dependent, estradiol-dependent or both. We did not observe modifications of the repertoire size (total number of different syllables produced by one individual) or the repertoire composition. The mean duration of the songs was not affected by the hormonal treatment, but three song parameters were significantly modified (Fig. 1). First, the duration of phrases was increased in both groups. Second, the number of different phrases per song decreased significantly in both groups of birds, with this effect significantly higher for the birds having both testosterone and estradiol available (T + Placebo). Finally, the rate of production of syllables along sequences was higher in T + Placebo birds, whereas this parameter was not changed in T + FAD birds.

### DISCUSSION

We have shown that steroid hormones influence song structure in canaries and that testosterone and estradiol seem to control distinct song parameters independently. We cannot reject the possibility that testosterone acts indirectly on the song system (i.e. transsynaptically) *via*, for example, the control of the catecholaminergic innervation of the song

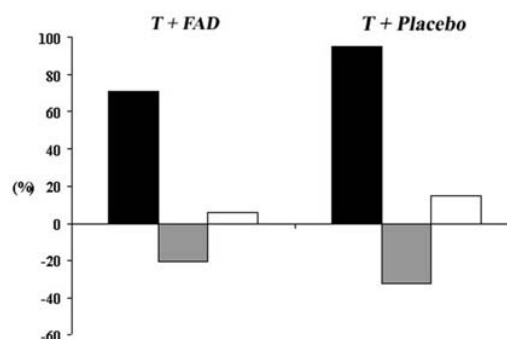


Fig. 1 – Changes (in %) in 3 song parameters after hormonal manipulation in the two groups of birds. The song parameters are: duration of phrases (black bars), number of different phrases per song (gray bars), and rate of production of syllables along sequences (white bars). The zero level refers to mean values obtained for these song parameters before hormonal manipulation.

system, as has been shown recently (Appeltants et al. 2003). However, the presence of receptors for testosterone and estradiol in the brain neural pathway that controls song production, especially in nucleus HVC, strongly suggests that the observed effects were mediated by a direct steroid action at the neuronal level. Furthermore, blocking the production of estrogens during testosterone-induced song development in adult female canaries also alters song patterns, and these effects are correlated with the inhibition of expression of estrogen-sensitive genes in HVC (Fusani et al. 2002).

### CONCLUSION

In canaries, the song produced by males is involved in both inter-sexual and intra-sexual relationships. Females of this species are especially responsive to certain song parameters, including the repetition rate of syllables (Vallet and Kreutzer 1995, Drăgănoiu et al. 2002), which is estradiol-dependent, as we have shown here. Therefore, it is possible that females rely on this parameter in the male songs to estimate the physiological state of their potential sexual partners. Further investigations are needed to determine the behavioral significance of other song parameters that we have shown to be under the control of steroid hormones.

# RESUMO

A influência da testosterona e do estradiol, respectivamente, na estrutura do canto do Canário-do-reino *Serinus canaria* foi estudada analisando o efeito da manipulação dos níveis sanguíneos de hormônios esteróides em machos nos parâmetros acústicos do canto. Uma análise detalhada dos cantos produzidos antes e depois da manipulação hormonal revelou que testosterona e estradiol parecem controlar independentemente parâmetros acústicos distintos. A presença de receptores para esses hormônios no circuito neuronal para controle da produção do canto sugere fortemente que os efeitos observados são mediados pela ação de esteróides a nível neuronal.

**Palavras-chave:** pássaros canoros, Canário-do-reino, canto, hormônios esteróides.

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